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# Comparative Physiology of Birds

E. A. HEWITT, D.V.M., PH. D.\*

THE structure and physiology of birds differs in many respects from that of mammals.

In general the muscles of birds correspond to those of mammals. There are some modifications, however, which seem to be more suited to the mechanism of the avian structure. There is a tendency in chickens and especially in turkeys toward extensive ossification of the muscle tendons. This tendency is particularly noticeable in the tendons of the legs but may also be observed in the tendons of the wing and neck in some cases. The breast or pectoral muscles and the wing muscles of the chicken and turkey are white, due to the relatively smaller amount of sarcoplasm in the muscle fibers. The muscles of the legs are of the red or dark variety which are rich in sarcoplasm. White muscles are more powerful but have less endurance than red muscles. In flying birds the pectoral and wing muscles are of the red variety.

## The Digestive System

The alimentary system of birds differs to a considerable degree from that of mammals. There is no provision made for mastication in the mouth owing to the absence of teeth. The beak is the prehensile organ by which food is taken into the mouth. The food is retained in the mouth only a short time. Salivary glands are present in the chicken but contain only mucous cells. According to some authors, the salivary glands of the woodpecker and goose produce a starch-splitting enzyme.

The pharynx extends from the row of papillae at the back of the hard palate to a row of papillae at the entrance to the esophagus. The esophagus is large and dilatable, thus serving to accommodate

the bulky, unmasticated food. It terminates in the proventriculus or glandular stomach. Near the thoracic inlet in many birds, the esophagus widens to form the crop. The portion of the esophagus anterior to the crop is similar in structure to the portion posterior to the crop. The structure of the esophagus is similar to that of mammals. It is characterized by a wide stratified squamous epithelial layer lining the organ. Mucous glands are found in the mucous membrane.

The food is swallowed almost immediately when it is taken into the mouth. The act of deglutition in birds differs in some respects from that of mammals. The lingual muscles are very poorly developed, except in the parrot. Owing to the rather rigid nature of the structures in the floor of the mouth and due to the absence of a mylohyoid muscle, it is impossible for swallowing to receive the muscular aid that it does in mammals. The bolus, therefore, instead of being pushed or shot into and through the pharynx by a contraction of the mylohyoid and other muscles is propelled backward by a raising of the head and giving it a quick forward thrust. It is of interest to note that when the mylohyoid muscle is paralyzed in mammals these animals likewise raise the head in swallowing. Investigators have found that the food, regardless of its consistency, is carried down the esophagus by peristalsis at an average rate of 1.5 centimeters per second. There is no evidence of squirting or shooting of the food down the esophagus as occurs with liquid or semi-liquid food in some mammals.

In insectivora, gulls and divers the crop is lacking. In palmipeds such as the duck and goose the crop forms only a spindle shaped enlargement. In pigeons the crop consists of a strong bilateral sacculatation. In the chicken and turkey it is unilateral

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and lies to the right of the median plane. In the chicken the mucous membrane of the crop contains a few mucous glands near the esophageal inlet; the secretion from these is fairly profuse. The lateral walls have a very rich blood supply, but this is not true in the lower wall; the scarcity of large blood vessels in the ventral wall is of considerable significance in operations upon the crop. The crop functions as a reservoir in which the food is softened and stored as long as the glandular stomach is in action. Some investigators claim that no digestive enzymes are secreted by the crop; others claim that an amylase is produced by the gland cells in the mucous membrane. Formerly, it was a common belief that gastric juice was regurgitated to the crop and that the food was partially digested there. Such a condition probably occurs only under pathological conditions. A few birds that feed their young with the crop contents can execute arbitrary vomiting movements. During this period of infant nursing the mother pigeon secretes the so-called crop milk. It is not a real secretion but consists of fatty degenerated, exfoliated epithelial cells. For this purpose the epithelium hypertrophies considerably. The thickness of the crop epithelium in pigeons normally is about 0.1554 mm. At the time the eggs are hatched the wall of the crop may increase in thickness up to 3 mm. in the mother pigeon according to Hasse. It is peculiar that male pigeons may prepare an acid crop milk in which colostrum-like corpuscles may appear. These corpuscles are not present in the product of the female pigeons. The moisture content of the crop ingesta is variable and seems to show no definite relation to the kind of food consumed or to the interval after eating.

The length of time that food remains in the crop varies mainly with the degree of filling of the organ. Browne found that if the different foods fed were of the same consistency there was little or no mixing in the crop and that they left the crop in the order in which they entered. However, if foods having different con-

sistencies were fed the softer food left the crop first. The greater the degree of filling the slower on the average did the food pass on from the crop. The crop presents two main types of movements; those that have to do with forcing ingesta into the proventriculus and those associated with hunger. The movements concerned with forcing food on are shallower and less energetic and also less rhythmic when the organ is full. In regard to the hunger contractions, many observations indicate that hunger returns shortly after eating. These hunger contractions probably occur as soon as there is any accommodation for food in the crop. It is stated that these hunger contractions begin 30 to 45 minutes after eating, the contractions gradually increase in frequency and vigor until in 5 to 6 hours they occur in groups of 6 to 12 or more, separated by intervals of comparative rest. When the crop is well distended with food only occasional contractions can be detected by the balloon method. An hour or so after eating periodic groups of hunger contractions begin. These gradually become augmented and motility becomes marked several hours after eating. It appears, therefore, that hunger contractions in birds, occurring in the crop, are similar to those occurring in the stomach of mammals. The contraction begins, however, when there is relatively more food present in the crop of birds than in the stomach of mammals.

The proventriculus or glandular stomach is a small, fusiform, glandular organ situated between the two liver lobes anterior to the gizzard and at the level of the two anterior renal poles. On casual examination it appears to be little more than a widened continuation of the esophagus but careful examination reveals that it is more than this. The epithelium of the esophagus becomes narrower and thinner as it approaches the proventriculus and changes at the junction into the one-layered, simple columnar epithelium found in the remainder of the digestive tract except in the anus. The mucous membrane is lined by simple columnar epithelial cells and is thrown into folds.

In the wall of the proventriculus there occurs two layers of glands: a superficial layer with tubular glands and a much heavier deep layer with compound tubular glands. The excretory ducts of the deeper glands open upon the surface between the superficial glands. Many mucous cells are found in the superficial glands. This corresponds with the fundus region of the mammalian stomach. The glands of the proventriculus secrete gastric juice. This juice is similar in composition to the gastric juice of mammals; pepsin, rennin and hydrochloric acid are present. The regulation of the secretion of gastric juice in birds is probably similar to that of mammals. Some investigators report that sham feeding causes a secretion which indicates a nervous mechanism at work, also several investigators report that chemical stimuli also play a part in the regulation of secretion.

Owing to the small size of the cavity of the proventriculus the food does not remain in this organ long. Therefore, the amount of gastric digestion taking place there must be inconsequential. Moreover, it has been pointed out that the relatively dry nature of the gizzard contents (average moisture content 44.2 per cent) makes it improbable that any considerable enzymic action goes on in that organ. These facts lend support to the idea that the duodenum is the probable seat of the main action of gastric juice. This view is strengthened by the fact that the reaction of the duodenum is always acid and that the alkaline pancreatic juice and bile enter the duodenum not near its origin but at its posterior extremity. In fact, the point of entry of the bile and pancreatic ducts is taken as the demarcation between the duodenum and ileum.

Posterior to the liver is the muscular stomach or gizzard. The segment of the alimentary tract between the glandular and muscular stomach varies in length. The deep glands of the proventriculus end abruptly and are followed by an increase in the length of the tubular glands of the surface. These soon take the characteristic aspect of the gizzard glands

and a keratinized layer appears above them. The gizzard is conspicuous by its biconvex form and its bright tendon sheets with which both surfaces are covered. According to Calhoun the muscular coat consists of a single thick layer of parallel fibers which extend from one aponeurosis to the other. Near the center of the tendinous aponeurosis the submucosa comes in contact with the tendinous aponeurosis and the muscular tissue is absent. Exterior to the muscle is a thin layer of connective tissue containing nerves and blood and lymph vessels. Elastic tissue is also present. Peritoneum covers the whole organ. The gizzard has as its innermost lining a horny layer which is about three-fourths as thick as the glandular layer adjacent to it. This horny layer is formed from an exudate or secretion of the glands. No digestive juice is secreted by the glands in the gizzard.

The gizzard is strongly developed especially in birds eating grain. In parrots, aquatic birds, ostriches, chickens and turkeys it is considerably larger than the glandular stomach. In birds of prey and birds eating fruits it is less developed. That the development of the gizzard is correlated with the kind of food eaten is indicated by the fact that geese fed meat have a smaller gizzard than geese fed grain.

The essential function of the gizzard is doubtless to crush and grind the coarse ingesta fed to it by the crop which acts as sort of a hopper for the gizzard. The grinding movements produce sounds which can be detected by auscultation. They are described as occurring at intervals of about 30 seconds. The pressure exerted by the contracting gizzard is considerable. It has been measured by means of a balloon inserted in the gizzard and connected by rubber tubing to a mercury manometer. Some average figures obtained are: hen, 138 mm. of Hg; duck, 178 mm.; and the goose 257 mm.

There is a widespread impression that in order for the gizzard to function properly it must contain grit which is

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thought to take the place of teeth. Many investigators have shown that baby chicks can be raised to maturity, utilizing their food, including whole corn and wheat without access to grit. On the other hand, other investigators have shown that adult chickens deprived of grit in their food, although having previously had access to it, retained grit in the gizzard for a period of 300 days or more.

The intestinal tract is shortest in birds of prey. In chickens, pigeons, ducks and geese it is four to five times as long as the entire body. In the ostrich it is nine times the length of the body. From the pylorus to the cloaca the entire intestinal tract is marked by the presence of villi and glands of Lieberkuhn. It contains much lymphoid tissue. The intestines have four divisions: the duodenum, the ileum, the ceca and the rectum. The ceca, two tubes with blind extremities, originate at the junction of the ileum with the rectum and extend toward the liver. The blind extremities are a good deal larger than the initial parts of the tubes. In the chicken each cecum is from 15 to 25 cm. long. In the pigeon they are only a few millimeters in length. Villi and tubular glands are present in the ceca.

The liver and pancreas are similar in structure to those of mammals. In the chicken each liver lobe has its separate bile duct. A gall bladder is absent in the pigeon, parrot, guinea and ostrich. Two pancreatic and three bile ducts open into duodenal papillae.

The spleen is small, brownish red, round, oval or somewhat disc-shaped. It lies to the right of the glandular stomach.

The metabolism of birds is very high. Small birds cannot remain alive very long without food. Ordinarily food amounting to 10 to 20% of the body weight is consumed daily. This fact is correlated with the high body temperature of birds and also with the fact that birds are always in motion when they are not sleeping or setting. This is fur-

ther correlated with the intensive work performed during the time of productivity. The total weight of eggs that are laid in a period of a few weeks frequently surpasses the weight of the body. During the time of laying the lime content of the blood is more than doubled.

The pancreatic juice contains enzymes similar to those formed by the pancreas of mammals. This is also the case of the intestinal juice. Protease, invertase and amylase are present in extracts of the mucous membrane obtained from the intestine as a whole. Amylase is present in cecal extracts but protease and invertase are said to be absent. The bile is similar in composition to that of mammalian bile.

The rate of digestion is relatively more rapid in birds than in mammals, especially in small birds. It is stated that the complete digestive process in small birds eating berries can take place in 10 minutes. A magpie may digest a mouse in 3 hours. Chickens require 12 to 14 hours in order to digest grain. Vegetable foods are digested somewhat less rapidly. Cellulose is digested very little or not at all. It is stated that the carbohydrate, starch flour, may be absorbed 100 per cent and albuminoid substances about 50 per cent.

The body temperature is from 40 to 43°C. (F. 104-109.4°). Small birds have the highest temperature. The average for the chicken is 40.8° C. (F. 105.2°) and for the pigeon 41.8° C. (F. 107.2°). While sleeping and especially while setting the body temperature drops and may be 2° less than the usual temperature. When the animal seeks food it uses only its organs of vision. Starved birds do not pick up food in the dark.

The cloaca is common to the digestive, urinary and genital apparatuses and represents the termination of these tracts. The rectum is separated from the cloaca by a constriction in the circular muscle which might be termed a sphincter. The cloaca is divided into three parts by transverse folds. These are the coprodaeum, the urodaeum and the proctodaeum. The ureters and genital tract open on the floor of the urodaeum. The

cloaca is lined with simple columnar epithelium. The anus is lined with stratified squamous epithelium.

### **The Respiratory System**

The nostrils which are holes through the upper mandible of the beak, have no membranes or movable alae. In water fowl the nostrils may be closed by a small valve. In other birds the nostrils are usually protected against the entrance of dust by small feathers or bristles. The nasal fossae open into the pharynx by a long, narrow slit behind the hard palate. In the duck an undivided space is located posterior to both nostrils. There are three turbinate bones. Birds possess an upper and lower larynx. The upper larynx corresponds to the larynx of mammals but has only a respiratory function and serves as an opening for the passage of air. It has no epiglottis but there is substituted a fold of mucous membrane. The absence of an epiglottis, however, does not prevent the complete occlusion of the glottis during the swallowing of food. The thyroid cartilage is lacking in the respiratory or upper larynx. The trachea has a large number of rings which are complete circles. The trachea of birds is peculiar in having longitudinal bands of extrinsic skeletal muscle fibers outside the cartilaginous rings. In many birds the trachea is remarkably long. The lumen of the distal part of the trachea is separated into two parts by a sagittal wall to form the inferior larynx or syrinx which is the organ of voice. It is a somewhat complicated structure, especially in song birds. Anterior to the bifurcation of the trachea the last three or six tracheal rings are modified to form a uniform osseous or cartilaginous drum. The muscular apparatus of the syrinx is firmly attached here. In many of the songbirds this muscular apparatus is more highly developed in the male than in the female. Sometimes the syrinx is expanded to form a bladder on one side or both. This bladder may be membranous or ossified as in the duck. The syrinx is attached by connective tissue to the esophagus.

The lungs are small and occupy only a portion of the thoracic space. They are closely applied to the dorsal surface of the thorax and present several deep indentations into which the ribs fit. The two principal bronchi into which the trachea is divided enter each lung about in the middle on the ventral surface. In the bronchi the cartilaginous rings are incomplete, and a portion of the wall is formed by a membrane. After entering the lungs the cartilage disappears. Each principal bronchus soon enlarges in the lung tissue to form the vestibulum which passes through the lung. This last part of the bronchus is called the mesobronchus. Near the caudal margin of each lung each mesobronchus is divided into two branches. Both end at the caudal margin of the lung in an air sac, one branch passes into the diaphragmatic or posterior thoracic air sacs and the other into the abdominal air sac. From the mediodorsal wall of the vestibulum there arise four to six ventral bronchi that lie in two rows. If the branches or rami of these bronchi have a diameter of 0.5 to 0.7 mm. they are called parabronchi or lung tubes. There are also numerous fine openings in the mesobronchi entering directly into the parabronchi. The wall of the parabronchi or lung tubes is provided with circular muscle fibers. Finally, the parabronchi ramify into numerous air alveoli. The alveoli freely anastomose with one another and are surrounded by blood capillaries. Some of the ventral bronchi open into the cervical and anterior thoracic air sacs. The ventral bronchi also divide into small canals that anastomose frequently with one another. The ventral system is connected by anastomoses with the dorsal parabronchial system. It is believed that the dorsal parabronchial system brings in the air and that the ventral system takes it out.

In birds the pulmonary mucous membrane is continued into cavities, designated as air sacs, which are developed between the walls of the thorax and abdomen on the one side and the thoracic and abdominal viscera on the other. The

air sacs are situated in such a manner that an early investigator (Carus) justly observed that the lungs of birds enclose all the other viscera. When the air sacs are distended with air they depress the viscera by pushing it toward the median plane. The air sacs are poorly supplied with blood vessels and nerves. They are mostly independent of each other but communicate freely with the lung by a single aperture and with the bones by one or more openings. The membranous wall of the air sacs is composed of two delicate layers, an external serous and an internal mucous layer; the latter is a continuation of the bronchial mucous membrane. The serous layer is a reflection of the pleura or the peritoneum.

Nine air sacs are usually described which are situated in the lower part of the neck and in the thoracic and abdominal cavities. A single anterior thoracic air sac is situated at the anterior part of the thorax and surrounds the inferior larynx, bronchi and large blood vessels of this region. It receives air from the anterior part of the lungs by two openings and communicates with air cells in the clavicle, coracoid, scapula and sternum, and also with deep seated air cells in the neck. There are two cervical or lateral thoracic air sacs which are situated at the base of the neck above the thoracic air sac. They lie in the inferior part of the neck and above the anterior part of the lung and extend along the cervical portion of the vertebral column up to the third cervical vertebra. They receive air from the internal edge of each lung opposite the base of the heart. They transmit air to the air cells in the vertebrae, ribs and humerus, and also to the air cells of the axillary region. There are four diaphragmatic air sacs usually described: two anterior and two posterior which are enclosed between the two diaphragmatic folds. Air is received from the lungs but is not transferred to bony structures from these receptacles. There are two abdominal air sacs, one on each side, extending from the lungs to the pelvic cavity. These are the largest in the

body. In chickens and waterfowl these sacs are highly developed. They are much less developed in song birds. These sacs supply air to the bones of the pelvic region such as the sacrum, coccygeal vertebrae and the iliac bones, and also to the femur in those species in which these bones are aeriased. The pneumatic conditions of the bones vary a great deal. Frequently the humerus, sternum, coracoid, pelvi and vertebra are pneumatic, rarely the femur. In birds of prey even the phalanges of the toes may be pneumatic. The wall of the air sac becomes very thin in the bones so that sometimes it can hardly be discerned. The absence of bone marrow in those bones is said to be due to the oxidizing action of the oxygen. The pneumatic condition of the bones may cause a considerable decrease in body weight. Less work then is required when the animals rise and fly. Furthermore, the air sacs help with the regulation of heat. In strenuous work such as flight they prevent over-heating because with the renewal of air much heat is eliminated. The anterior air sacs also send processes into the bones between the pectoral muscles. There are some birds in which quite extensive air sac processes extend as far as the subcutis.

The mechanism of respiration differs in many respects from that of mammals. The slight mobility of the vertebral ribs and the adhesion of the lungs to their inner surfaces allows only a slight dilatation of the lungs during inspiration. The diaphragm does not exhibit the muscular development that is found in mammals. It is principally membranous with fine muscular bundles attached to the ribs. Two thin delicate membranes compose the diaphragm and divide it into two planes, a pulmonary and thoracic-abdominal plane. The pulmonary plane is spread over the inferior surfaces of the lungs and is attached to the ribs on its border. The thoracic-abdominal plane has its origin on the dorsal wall in common with the pulmonary plane. It is convex anteriorly and extends to the

sternum. The entrance of air into the pulmonary tissue is effected by a dilatation of the diaphragmatic air sacs, the position of which effectively allows for their expansion. By the action of the respiratory muscles such as the serratus ventralis and external intercostals the inferior ribs are drawn outward and the posterior part of the thorax is widened. Since the lungs are located on the dorsal ends of the ribs they must join in the movements of the ribs. To this movement is added the function of the costopulmonales muscles of the diaphragm whereby the lateral margins of the lungs are expanded with the distention of the diaphragmatic air sacs. This action takes place with each inspiration so that the lateral ramifications of the bronchi enlarge while the medial parts of the lung, where the ramifications of the ventral bronchi pass, are pressed together. The air arrives in the diaphragmatic air sacs partly pure and partly altered by the exchanges with blood in the capillaries surrounding the alveoli. The abdominal air sacs act as antagonists to the diaphragmatic sacs, decreasing in size during inspiration and increasing in size during expiration. As a result the air contained in these sacs is chiefly vitiated air. In expiration some of the air in the diaphragmatic sacs is forced into the ventral bronchial system some of which in turn finds its way into the anterior air sacs. Also some of the air in the diaphragmatic sacs passes out over the same course that it pursued in entering. Thus, this air is exposed to the diffusion exchanges in the pulmonary tissue a second time. The gaseous transformation accomplished in the lung takes place during the two acts of respiration, inspiration and expiration. The air in the anterior sacs and probably to a great extent in the posterior sacs is aided in expulsion by the flapping of the wings. The functions of the air sacs extend beyond that of respiration as they are concerned in locomotion by diminishing the weight and by their position in rendering equilibrium more stable. They are also concerned in the produc-

tion of voice sounds, the range and power of which they augment.

### **The Blood and Circulation**

The heart of birds is cone shaped and is placed in the anterior extremity of the thoracic cavity. There are two anterior vena cavae as well as one posterior vena cava which terminate in the right atrium. A peculiarity of the heart in birds is the absence of a tri-cuspid valve at the right atrio-ventricular opening; instead there is a strong muscular fold which becomes closely applied to the ventricular septum during systole to prevent the regurgitation of blood into the atrial cavity. There are two pulmonary veins which empty into the left atrium. The left atrio-ventricular opening is provided with a bi-cuspid or mitral valve.

Two important differences between avian and mammalian blood are the presence of nuclei in the red corpuscles in the avian blood and the elliptical shape of these cells. The normal number of corpuscles is about 3,250,000 red blood cells and about 26,000 white blood cells per cubic millimeter of blood giving a ratio of 125 to 1.

### **The Nervous System**

There are a few modifications of the nervous system of birds as compared with mammals which are of considerable interest. The cerebral hemispheres of the brain are well developed but have a relatively smooth surface in contrast to the convoluted surface observed in the cerebrum of mammals. The cerebellum is conspicuous by the smallness of the lateral lobes. The optic lobes are in a lateral, inferior position at the sides of the cerebellum. The paramount importance of the visual apparatus is indicated by the large size of the optic chiasma. The diameter of the optic nerve is about equal to that of the spinal cord in its dorsal region. The olfactory lobes are relatively small. There is an absence of nervous tracts leading to the spinal cord from the cerebrum. The cerebrum does, however, exert an influence over the



rest of the nervous system through its nervous tracts connecting it with other divisions of the brain. If the cerebral hemispheres in a chicken are removed the animal evidences no marked defect of movement. However, such an animal is not sensitive to light or sound. It will not pick up grain and must be fed. Such an animal can walk around and avoid obstacles. Its ability to perch and maintain its equilibrium is not lost.

### BANG'S VACCINATION—

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mative answers to the following questions, or to make due deductions if negative answers are indicated:

1. Have enough animals been used to make sure that the results have not been clouded by the unavoidable selection of natural immunes and semi-immunes?
2. Have sufficient numbers of controls been employed?
3. Do the vaccinates and controls in-

clude reasonably well-defined groups as regards age and condition (calves, non-reacting open cows, reacting open cows, etc.)?

4. Has there been natural exposure, capable of infecting controls regularly?

5. Are there accurate data on the blood titer of all animals, on their status as spreaders from the milk and genital tract, on the abortion rate, and on the reproductive efficiency?

6. Has the experiment been continued long enough to provide data on the duration of the immunity that is established?

7. Has the strain used in preparing the vaccine been carefully checked to insure the employment of smooth cultures?

Obviously, these questions do not furnish in detail a complete criterion on which to base our judgment. They do, though, include essential points, for any one of the number, omitted, would seriously diminish or completely destroy the value of an experiment designed to determine the immunizing power of a vaccine.

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